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TRANSACTIONS

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AMERICAN ENTOMOLOGICAL SOCIETY

VOLUME LXXIX

ON TWO INTERESTING PHASMIDS (ORTHOPTERA: PHASMATIDAE) FROM COASTAL PERU

BY JAMES A. G. REHN

Curator of Insects, Academy of Natural Sciences of Philadelphia

Dr. Wolfgang Weyrauch, of Lima, Peru, recently sent to me for determination material of both sexes of two species of phasmids from the general Lima area. One of these proves to be an undescribed member of the genus *Libethra,* the other a previously, but insufficiently, described and unfigured species of the genus *Bostra.* Our knowledge of the numerous previously described species of both of these Neotropical genera is limited and unsatisfactory, and of both many forms undoubtedly yet remain to be made known. As with many phasmids much of the difficulty is due to their marked sexual dimorphism, as a result of which sexes of the same species have occasionally been referred to distinct genera.

Dr. Weyrauch wishes to use the names of these species in a study now under way, and the present paper has been prepared to facilitate his work.

Libethra minuscula [1] new species (Pl. I, figs. 1, 2, 5 and 6.)

This very distinctive species would fall into what Günther regards as the *nodosa* group of the genus,[2] which he distinguishes

[1] In allusion to its small size.

[2] Mitt. Zoolog. Mus. Berlin, 18, heft 2, p. 258, (1932). This paper has much of constructive value in it, but in a number of instances the author has incorrectly associated species he had never seen, and assigned tentative racial status to others, which from type evidence are clearly very distinct species.

from his *strigiventris* group by the male sex having the distal margin of the poculum emarginate mesad. However, this is an exceedingly arbitrary arrangement, as various members of what he regards as the *strigiventris* group differ from one another much more widely by other features, some of which are ambisexual. His so-called *nodosa* group lacks sufficient value to be maintained even as a convenience entity, and its species should be grouped with those regarded by him as members of the *strigiventris* group.

From the three species placed in Günther's *nodosa* group, i.e. *nodosa* (Giglio-Tos),[3] *palmes* (Giglio-Tos),[4] and *spinulosa* Brunner,[5] the present one differs from all in having one or two small but distinct spaced spines distad on the ventral carinae of the median and caudal femora, and also in the male sex by having the ventro-distal angle of the penultimate tergite with a definite peg-like process. Further it is much smaller than *nodosa* (♂ body length, 52 mm.), and very much smaller than *palmes* (♂ body length, 67 mm.), and it also differs from the former in having the caudal margin of the pronotum transverse truncate instead of rounded, in the apex of the poculum of the male not reaching as far caudal as the distal margin of the penultimate tergite (Giglio-Tos' segment VIII), and in its quite different coloration. From *palea* it also differs in the distal margin of the ultimate tergite of the male (anal segment) not being emarginate mesad. From *spinulosa* Brunner *minuscula,* while of more nearly similar size, can also be distinguished by the fewer granulations of the head and thorax, by the virtual absence of denticulations from the distal margins of the abdominal tergites, and by the apparently less compressed character of the poculum of the male sex, which is described for *spinulosa* as compressed-cucullate.

Of the species assigned by Günther to his *strigiventris* group *minuscula* is apparently nearest to *L. molita* (Westwood),[6] *L.*

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[3] *Bacunculus* (?) *nodosus* Giglio-Tos, Boll. Mus. Zool. Anat. Comp. Univ. Torino, XIII, no. 311, pp. 21, 27 (1898). [♂; Gualaquiza, Ecuador.]

[4] *Libethra* (?) *palmes* Giglio-Tos, Boll. Mus. Zool. Anat. Comp. Univ. Torino, XIII, no. 311, p. 28 (1898). [♂; Gualaquiza (type locality) and Valley of Santiago, Ecuador.]

[5] Insektenf. Phasm., II, pp. 304, 307 (1907). [♂; Ecuador.]

[6] Catal. Orth. Ins. Brit. Mus., Phasmidae, p. 29, pl. XXIV, figs. 3, 3a and 3b (1859). [♂; Colombia.]

metae Hebard[7] and *L. straminea* Hebard.[8] From all of these, as from the members of Günther's *nodosa* group, *minuscula* differs in the spined ventral margins of the median and caudal femora, as well as in its stockier form in the male sex and the divided margin of the poculum in the same. Comparison has been made with material of *molita* which fully agrees with Westwood's description, and which was so recorded by Hebard,[9] while comparisons have also been made with the types of the latter author's *metae* and *straminea.* From *metae* in the male sex *minuscula* can further be distinguished by its smaller size, less slender build, apically blunter cerci, nodose ventro-caudal angles of the penultimate abdominal tergite, and the emarginate and strongly labiate distal margin of the poculum, while in the female sex it can at once be distinguished by its acuminate ultimate abdominal tergite and lanceolate and non-emarginate operculum. From *straminea* the present species is also distinguishable by its less attenuate body, the blunter cerci, nodose ventro-caudal angles of the penultimate abdominal tergite, and the different pattern of its male poculum, which is much less cymbiform in *straminea.* Westwood's *molita* is over twice the size of *minuscula,* has a much more attenuate body, somewhat similar nodosities ventro-caudad on the penultimate tergite, and a compressed and spout-like apex to the male poculum, which latter is also non-labiate and more compressed than in *minuscula,* while the more distal abdominal tergites in the same sex lack the spaced and conspicuous longitudinal strigae seen in *minuscula.*

Type.— ♂ ; Quebrada Verde, between Lima and Lurin,[10] Department of Lima, Peru. 1950. (W. Weyrauch.) [Academy of Natural Sciences of Philadelphia, Type. no. 5771.]

Size small (for the genus) ; form much less attenuate than in the same sex of many species of the genus; surface of head and pronotum with a

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[7] Trans. Amer. Entom. Soc., LIX, p. 39, pl. III, fig. 3 (1933). [♂ (type), ♀ ; Villavicencio, Meta, Colombia.]

[8] Trans. Amer. Entom. Soc., LIX, p. 38, pl. III, fig. 2 (1933). [♂ ; Bogotá, Cundinamarca, Colombia.]

[9] Trans. Amer. Entom. Soc., XLV, p. 169 (1919). Material from Cunday, Tolima, and Villa Eloira and San Antonio, Cauca, Colombia.

[10] Lurin is a coastal community approximately twenty miles in an air-line southeast of Lima, with which it is connected by highway and railroad.

moderate number of scattered nodulose points, some not symmetrically disposed, none long enough to be spiniform, abdomen with five longitudinal strigae on the more distal tergites, these becoming subobsolete on the more proximal ones, particularly the median striga, proximal section of more proximal tergites each with a median pair of closely placed rounded nodules, on some tergites these supplemented by similar low nodules proximad on the subobsolete longitudinal strigae.

Head with its greatest length subequal to that of the pronotum, greatest breadth across eyes equal to 1.2 times the greatest breadth of the pronotum, evenly narrowing caudad of the eyes; middle line of occiput with a contiguous pair of low rounded but quite distinct tubercles, in addition to which more laterad and caudad are three pairs of nodules; eyes faintly flattened as seen from dorsum, their basal outline longitudinally ovate. Antennae reaching at least as far caudad as the apices of the caudal femora.[11]

Pronotum with its greatest breadth equal to faintly more than two-thirds of its length (as 10 to 14), cephalic and caudal margins subtruncate, the lateral margins faintly outbowed over the insertion of the cephalic limbs, medio-longitudinal sulcation distinct but slight, transverse one situated faintly cephalad of the middle and weakly obtuse-angulate; mesonotum slightly shorter than the median femora, roughly subequal in breadth except for the caudal expansion dorsad of the insertion of the median limbs, surface with numerous scattered, small and very low nodulose tubercles or granules, which are only in part disposed symmetrically; metanotum (with median segment) virtually three-fourths as long as the mesonotum, faintly broader, median segment equal to slightly more than one-third the length of the metanotum exclusive of the median segment, the latter slightly longer than broad, surface of the entire metazonal section with scattered tubercles or granules as on the mesonotum.

Abdomen with most of the tergites bearing proximad a median closely placed pair of low rounded tubercles, these accompanied laterad on tergites three to six by an additional pair of similar tubercles, while there is progressively evident distad a pattern of carinulations, which are quite marked and trilineate on tergites eight and nine, plus lateral submarginal carinulae, tergites three to six subequal in length, seventh slightly shorter, eighth subequal to seventh in length and very feebly expanded laterad, ninth tergite compressed, narrower than eighth, its disto-ventral angles each with a marked dentiform peg directed ventro-distad; anal segment three-fourths as long as ninth tergite, moderately bullate inflated dorso-laterad as in all the related species, its distal margin virtually straight as seen from the dorsum, and as viewed in caudal aspect obtuse-angulately vaulted; cerci relatively short, moderately stout, inbowed, their apices bluntly rounded and supplied with numerous minute denticles; poculum markedly failing to reach as far

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[11] In the type, which has the male genital characters in better shape, the antennae are incomplete, and this information has been drawn from a paratype.

caudad as the distal margin of the ninth tergite, relatively broad, cymbiform, its dorsal margin proximad with thickened, laterad projecting strumosities, while the distal portion of the margin is broadly produced into a labiation which is shallowly emarginate mesad.

Cephalic femora but faintly shorter than the combined length of the pronotum and mesonotum, carinae marked; cephalic tibiae quite slender, slightly longer than the femora. Median and caudal femora each with one or two (usually two) inclined teeth distad on their ventro-lateral carinae, the remainder of the latter unarmed, as is the medio-ventral carinula of each, median femora slightly longer than the mesonotum, median tibiae subequal to the femora in length, caudal femora 1.2 times as long as the pronotum and mesonotum combined, reaching caudad as far as the distal margin of the seventh abdominal tergite, somewhat more slender than the median ones, caudal tibiae slightly longer than the femora, as slender as the median ones, caudal metatarsus slightly longer than the remaining caudal tarsal articles together.

Allotype.— ♀ ; same data as type. [Academy of Natural Sciences of Philadelphia.]

Size as small proportionately as in the male sex; form more robust (as usual in females of this genus), limbs relatively short; surface of head and thoracic sections with numerous yet generally low tubercles or granules, these often symmetrically disposed, abdomen with some less evident granules, and a longitudinal type of strigation suggesting that of the male but as a whole more subdued, and also on several of the more proximal tergites a transverse distal marginal series of lobulations.

Head with its length equal to 1.3 times that of the pronotum, greatest breadth across eyes subequal to the pronotal length, in outline somewhat narrowing caudad of eyes, in addition to several well-marked more lateral and caudal subspiniform tubercles the middle of the occiput bears a pair of erect contiguous subbulbous and auriform lobes, which in height are subequal to the longitudinal dimension of the eye; antennae reaching caudad to the third abdominal tergite.

Pronotum with its greatest breadth equal to seven-eighths of its length, its cephalic and caudal margins arcuato-truncate, in form the pronotum slightly widens caudad, surface with the most evident of its tubercles a pair placed mesad near the caudal margin, others largely sublongitudinal in disposition, medio-longitudinal sulcation faint, transverse one more marked, arcuate and mesad in position; mesonotum four times as long as the pronotum, evenly broadening caudad, its greatest breadth briefly preceding the caudal margin and contained 2.3 times in the mesonotal length, tubercles of the intra-marginal longitudinally disposed lateral series larger than the more discal ones, which latter as a whole are less symmetrically disposed, mesopleural tubercles with a spaced ventral intra-marginal series and a shorter, more dorsal and juxta-coxal one composed of larger tubercles than the others on the

mesopleura; metanotum, with the median segment (proximal abdominal tergite), equal in length to slightly more than seven-tenths of that of the mesonotum (as 35 to 48), the breadth slightly greater than that of the mesonotum caudad, at its greatest width equal to five-sevenths of its length, median segment transverse, and with its length slightly less than one-half that of the remainder of the metanotum (as 11 to 24), greatest breadth of the median segment equal to 2.25 times the length of the same, surface of the metanotum as a whole with a more longitudinal disposition of the tubercles than is true of the mesonotum, the larger ones present laterad and across the caudal margin of the true metanotum, metapleural tubercles less pronounced but rather similar in disposition to those of the mesopleura.

Abdomen moderately stout proximad, evenly narrowing distad, proximal tergites transverse in general proportions, the more median ones subquadrate in outline, seventh and eighth more longitudinal, the ninth nearer quadrate, second and third tergites with distal intra-marginal transversely disposed series of rather low lobules mesad, these passing laterad to tubercles, the third tergite with the median two pairs of lobules more marked than any others, increasingly less evident traces of these lobules and tubercles on the fourth to sixth tergites, while on the seventh to ninth a longitudinal pattern of strigae suggests that found in the same area in the male sex but here less strongly emphasized; anal segment lanceolate in outline as seen from dorsum, but faintly longer than the ninth tergite, its margins, in the same view, subarcuately converging to the narrowly rounded acute apex, as seen in profile with its dorsal line faintly concave declivent to the apex, to which the ventro-lateral margins are obliquely ascendant, dorsal surface with a well-marked medio-longitudinal carina, as well as a pair of less evident more lateral ones which are subconvergent distad but fail to reach the margin of the segment. Cerci hidden under the anal segment. Operculum moderately elongate, reaching as far caudad as the proximal third of the anal segment, in outline relatively broad lanceolate, the apex moderately acute, ventral surface distad shallowly carinate medio-longitudinally.

Limbs all relatively short. Cephalic femora a little shorter than the combined length of the pronotum and mesonotum, carinae well developed, basal flexure occupying approximately two-fifths of the femoral length; cephalic tibiae faintly longer than the femora, well carinate, moderately compressed. Median and caudal femora with one or two (usually two) ventral marginal lobiform teeth distad; median femora somewhat shorter than the mesonotum, strongly carinate, moderately compressed; median tibiae faintly longer than the femora; caudal femora reaching caudad as far as the middle of the sixth abdominal tergite; caudal tibiae surpassing the femoral length by a distance subequal to the length of the coxa and trochanter; caudal tarsi with metatarsus three-fourths as long as the remaining tarsal articles together.

Measurements (in millimeters)

	Length of body	Length of antenna	Length of pronotum	Length of mesonotum	Length of metanotum (incl. med. segm.)	Length of cephalic femur	Length of median femur	Length of caudal femur
♂, Quebrada Verde, Peru, *type*	33.0	18.7[12]	2.2	7.8	5.7	10.9	8.6	12.2
♂, Lima, Peru, *paratype*	38.0	33.4	2.4	9.6	7.0	14.1	10.5	14.3
♀, Quebrada Verde, Peru, *allotype* ..	44.3	23.6	3.0	9.4	6.1	11.4	8.1	11.2
♀, Quebrada Verde, Peru, *paratype* ..	46.0	23.0	2.9	9.9	6.5	11.0	8.9	11.7

Coloration.—This species has at least two well-marked color phases in each sex, probably with intermediate conditions in both, as here noted for the female.

Males. Phase A (to which the type and the male topotypic paratype belong): almost entirely dark olive-gray (of Ridgway), paling to mineral gray proximad on the median and caudal femora, while the tibiae are speckled with the same, and the dorsal surface of the abdomen pales in areas to light olive-gray, the antennae obscurely subannulate with the paler tone distad. Phase B (the Lima male): almost uniformly clay color, darkening to snuff brown on apex of abdomen, tibiae becoming ochraceous-buff.

Females. Phase A (to which the allotype alone belongs): base color pale yellow-green (of Ridgway) overlaid with a strongly variegated pattern of maculae, annuli and clouds of fuscous-black, these being more or less complete annuli on the elements of the limbs, plus well-marked but rather irregular blotches on the occiput, genae, cephalic half of the pronotum, a medio-longitudinal dash caudad on the pronotum and cephalad on the mesonotum, a transverse cloud at the caudal fourth of the latter and others on the metanotum, median segment and the other more proximal abdominal tergites, following which the abdominal tergites have more lateral paired caudo-dorsad converging irregular blotches; pleura heavily sprinkled with many points of fuscous-black; venter of abdomen with fuscous-black points, as well as others in the gular region, and on the sternal elements, operculum with a medio-longitudinal line of fuscous-black; antennae largely annulate rather irregularly with the light and dark color tones. Phase B (extreme in one paratypic female and approached in two others): general tone light drab to grayish olive (of Ridgway) obscurely clouded with hair brown, the annuli of the limbs seen in type A but faintly marked, the median and caudal femora clearer pale proximad, the dorsum of the abdomen darkened

[12] Incomplete.

proximo-mesad, the operculum dark medio-longitudinally proximad, antennae with distinct dark annuli only distad. The two other females, considered here as more nearly approaching type B, are more heavily infuscate than the extreme of the latter and one shows definite dark annuli on the median and caudal limbs, while the other has the same heavily infuscate, except proximad on the caudal femora, and with little if any trace of annuli.

Remarks.—In addition to the type and allotype I have before me three paratypic females and one paratypic male bearing the same data as the type, and a single male, also regarded as a paratype, taken at Lima, Peru, August 12, 1914, by H. S. Parish, and in the collection of the Academy of Natural Sciences of Philadelphia. The species is clearly dichromatic, this especially marked in the female sex. The females before me also show that, as in certain related genera, the paired occipital lobes vary individually in their degree of development and exact shape. In one female they are indicated only as the merest nodules, no greater in size than others on the occipital surface, while in another they are even more prominent than in the allotype, the remaining female with an intermediate development between that of the allotype and of the one showing the minimum-sized structures. The present series, taken together under similar conditions, demonstrates very clearly the unreliability of such lobar development as specific criteria in this and related genera.

Bostra scabrinota Redtenbacher (Pl. I, figs. 3 and 4.)

1908. *B*[*ostra*] *scabrinota* Redtenbacher, in Brunner and Redtenbacher, Insektenf. Phasm., III, pp. 407, 410. [♀; Lima, Peru.]

Quebrada Verde, between Lima and Lurin, Peru; 1950 (W. Weyrauch); 1 ♂, 1 ♀.

The female here reported shows sufficient points of agreement with the original description of this species—which was based solely on that sex—for me to regard it as representing *scabrinota.* As is the case with most of the descriptions in "Die Insektenfamilie der Phasmiden," that of this species is far too brief for members of groups as basically difficult as the phasmids. However, the present female shows certain differences from the description which I would regard as purely individual, although worthy of note to aid future students. The head lacks paired spines, which were said originally to be closely placed between the

eyes, but we know that in certain genera there is plasticity within species in this respect, as in the case of the here-described *Libethra minuscula*. The mesonotum and metanotum totally lack a median carina, although the former has numerous obtuse spines, and cephalad the metanotum also has a few shorter and less evident ones. The femora of the median and caudal limbs have very low rounded lobations distad on their ventro-lateral margins, in the median femora solely on the cephalic side, in the caudal ones on both sides; however, neither of the dorso-lateral carinae are lobate or spined.

The male, previously undescribed and hence the allotype, has a distinctive type of anal segment, which does not seem to be paralleled in any other described species of this genus. This is developed disto-laterad into peg-like processes which are directed ventrad and the apices of which are armed with a group of minute denticles. The following description and the accompanying figures should prove of service to other students.

Allotype.—♂; Quebrada Verde, Peru. 1950. (W. Weyrauch.) [Academy of Natural Sciences of Philadelphia.]

Form very elongate and slender; surface as a whole smooth.

Head faintly shorter than the pronotum (as 17 to 18), slightly and evenly narrowing caudad, no surface tubercles except a median subobsolete, very low and rounded pair of nodules at the caudal border; eyes but moderately prominent, broad ovate in basal outline, their length subequal to half that of the postocular portion of the head; antennae elongate, extended caudad their apices reach to the distal margin of the sixth abdominal tergite, all articles except those at base and in distal fifth very attenuate, proximal article moderately flattened, but faintly longer than the second.

Pronotum with its greatest median breadth contained 1.7 times in its length, cephalic margin truncate, caudal margin arcuato-truncate, transverse impression well marked and median, cephalic half of pronotum laterad with well-marked intra-marginal longitudinal subsinuate impressions. Mesonotum very slender, 5.1 times as long as the pronotum, its greatest breadth caudad contained 10.3 times in its length, its average breadth 14.25 times in the length, no distinct median carinula present, but a very faint medio-longitudinal tectation is indicated except at the extremities. Metanotum (with median segment) three-fourths as long as the mesonotum, similar in build and breadth, median segment (proximal abdominal tergite) less than one-third as long as metanotum including the median segment (as 25 to 86), itself much longer than broad, the segmental length being 2.5 times its greatest breadth, which is caudad.

Abdomen slender, as a whole subequal in breadth, its surface smooth, tergites two to six approximately subequal in length, seventh tergite two-thirds as long as the sixth, faintly more slender, eighth tergite much shorter, its lateral length equal to but half that of the seventh, moderately broadening distad, its distal margin arcuately concave and connected with the ninth tergite by a membrane which fills the concavity; ninth tergite in length equal to three-fifths that of the seventh, its breadth equal to that of the distal portion of the eighth, proximad sellate and laterally constricted dorsad of the lateral margins, moderately bullate distad in both dorsal and lateral aspects, distal margin transverse truncate; anal segment with its length but half that of the ninth tergite, in profile oblique declivent, the disto-lateral angles produced ventrad into relatively stout styliform pegs, the bluntly rounded apices of which bear minute recurved denticles, distal margin as seen from the dorsum weakly obtuse-angulate, a shallow medio-longitudinal carinula indicated, the surface laterad of this distally subexcavate; supra-anal plate little evident distad of anal segment, transverse, its margin low arcuate. Cerci simple, directed ventrad, markedly incurved in distal two-fifths, slightly thickened and subclavate at the bluntly rounded apices. Poculum reaching distad as far as the apex of the supra-anal plate, its slightly narrowed distal section having the apical margin very faintly emarginate mesad, ventral surface of poculum with its proximal margin mesad semi-elliptically concave-emarginate, this area filled with membrane, the margins of this diastema elevated—and particularly mesad—into a sublamellate border, the surface distad sellately concave, while about this area the cerci are normally clasped.

Limbs exceedingly slender, of the type usual in this genus, without marginal lobes or marked spinules; cephalic femora 1.3 times as long as the mesonotum, cephalic flexure well marked, cephalic tibiae nearly 1.3 times as long as the femora; median femora but faintly shorter than the cephalic ones, median tibiae slightly more than 1.2 times the femoral length; caudal femora subequal to the cephalic femora in length, caudal tibiae slightly more than 1.35 times the femoral length; caudal tarsi incomplete.

Coloration.—Tone of the sides of the body citrine-drab to deep olive, this passing distad on the abdominal tergites to pencilled longitudinal intramarginal linings of fuscous, middle of dorsum of thorax and abdomen washed with brick red, apex of abdomen and head lightening to cream color, the latter with dull darker postocular bars which also extend over the pronotum; cephalic and median limbs with base tone ranging from cinnamon-buff to antimony yellow, cloud annulate with fuscous; caudal limbs with base color nearer testaceous with similar obscure cloud annuli; antennae distad of the two proximal articles solidly dark olive.

Measurements (in millimeters)

	Length of body (exclusive of operculum)	Length of antenna	Length of pronotum	Length of mesonotum	Length of metanotum (incl. med. segm.)	Length of cephalic femur	Length of median femur	Length of caudal femur	Length of operculum
♂, Quebrada Verde, Peru, *allotype* ..	67.5	59.0	2.4	18.0	13.6	24.4	23.0	25.2	—
♀, Quebrada Verde, Peru	87.5	45.5	4.5	23.0	15.5	23.0	18.0	23.0	16.2
♀, Lima, Peru, *type* (ex Redtenbacher)	80.0	—	—	19.0	13.0	22.0	18.0	22.0	—

Explanation of Plate I

Fig. 1.—*Libethra minuscula* new species. Male (type). Between Lima and Lurin, Peru. Lateral view of apex of abdomen. (Greatly enlarged.)

Fig. 2.—*Libethra minuscula* new species. Male (type). Between Lima and Lurin, Peru. Dorsal view of apex of abdomen. (Greatly enlarged.)

Fig. 3.—*Bostra scabrinota* Redtenbacher. Male (allotype). Between Lima and Lurin, Peru. Lateral view of apex of abdomen. (Greatly enlarged.)

Fig. 4.—*Bostra scabrinota* Redtenbacher. Male (allotype). Between Lima and Lurin, Peru. Dorsal view of apex of abdomen. (Greatly enlarged.)

Fig. 5.—*Libethra minuscula* new species. Female (allotype). Between Lima and Lurin, Peru. Lateral view of apex of abdomen. (Greatly enlarged.)

Fig. 6.—*Libethra minuscula* new species. Female (allotype). Between Lima and Lurin, Peru. Dorsal view of apex of abdomen. (Greatly enlarged.)

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REHN—PHASMIDS FROM COASTAL PERU

BIOLOGY OF EUMENINE WASPS I. THE ECOLOGY, PREDATION, NESTING AND COMPETITION OF *ANCISTROCERUS ANTILOPE* (Panzer)

BY KENNETH W. COOPER

E. N. Huyck Preserve, and University of Rochester, N. Y.

Most of the scant knowledge that we possess today of the biology of our eumenine wasps has been derived from more or less isolated, fragmentary, chance observations made by a relatively small number of naturalists, chief among whom are the Peckhams, Hartman, Rau, and Reinhard. As useful and valuable as much of the information is, the mode of its collection seems to have had the unfortunate consequence of creating a widespread feeling among biologists that a detailed study of the life history of one or more species would require so much luck, happy coincidence, ingenuity and endless effort, as to be an unreasonable undertaking. Very likely this is so if a search for nests in nature be the sole basis for study. Nevertheless species that live in hollow stems, reeds, wood borings, and other already prepared cavities, do in fact represent material admirably suited for the experimental study of problems of distribution and ecological domain, predation, mortality rates, competition, nesting factors, and so on, even though their natural nests may rarely be found.

During an attempt to discover the nature of the remarkable association between the wasp *Ancistrocerus antilope* (Panzer) (= *capra* Sauss.) and a mite whose deutonymph is commonly found riding the propodeum of the male wasp, an intensive but fruitless search was made for the wasp's nest in regions where the female wasp abounded and had been observed with prey. Taylor's (1922), Balfour-Browne's (1925) and March's (1930) [1] success in enticing *A. antilope* to nest in glass tubes enclosed in wood, or

[1] March gives insufficient information. He may have mistaken a number of different eumenine wasps, and it is possible that he did not in fact observe *A. antilope* at all.

paper, suggested the use of simple borings in easily-split, straight-grained wood. In this case the high egg, larval and pupal mortality brought about by condensation of moisture on the glass walls would be avoided, along with subsequent bacterial and mold infections, and it seemed a more simple matter to get at the occupants of the burrows by splitting the wooden sticks. So indeed it proved and, for example, 77 of 131 trap-nests (having burrows from 95-120 mm long and 6 or 7 mm wide), placed in *A. antilope*'s special haunts in July, were closed by nesting insects within 2 to 31 days. Eumenid wasps were the predominant inhabitants, and *A. antilope* was by far the most frequent resident. Depending on the dimensions of the burrow, the site and mode of placement of the trap-nest, and the seasonal period, these borings in wood were accepted and nested within by a number of species of *Ancistrocerus, Symmorphus, Stenodynerus* and *Rygchium* among the Vespidae, as well as *Trypoxylon* and some other wasps, and a surprising number of bees; a miscellany of ants, caterpillars, spiders, isopods, *Polyxenus,* and so forth, also nested or sheltered within them. Had the 131 nests been of other dimensions, or placed in other situations, different spectrums of inhabitants and other dominant species would have been expected.

The well-planned use of trap-nests proves a ready means for gaining answers to many questions about these wasps and their associates that interest biologists today. Certainly it made feasible the discovery of the interrelations between *A. antilope* and its mite, an account of which will be reported separately. The following notes are an outcome of that study, and provide a background of information about the wasp's nest, its provisions, and a time-table of the wasp's developmental stages, all so necessary for understanding the world in which *A. antilope's* mite spends its adult life.

The Occurrence of the Wasp

Ancistrocerus antilope is a Holarctic wasp, found throughout most of the United States and southern Canada, as well as in the British Isles, Europe and Asia. In upland, partially wooded farming areas of eastern New York, it is by all odds the commonest eumenine wasp, and our largest species of *Ancistrocerus.* Thus,

in a collection of 704 eumenines made for the purpose of a census of the various species in the vicinity of Rensselaerville, N. Y. (at ca. 1500 ft. elevation), during late June, July and August, 24 species of Eumeninae are represented. *A. antilope* composes nearly a quarter (171 specimens, or 24%) of the total sample, and is only rather distantly followed by the other three most common species: *A. tigris* (Sauss.) (14%), *Rygchium foraminatum* (Sauss.) (13%), and *Symmorphus canadensis* (Sauss.) (11%). Males constitute 64% (100 individuals) of the specimens of *A. antilope*. The skewed sex ratio may be owing to the fact that male wasps spend longer periods visiting flowers than do females, and most wasps of the census sample were taken at flowers.

A. antilope is only rarely found within stretches of open fields, and—in my experience—not at all within close-grown deciduous woods, or coniferous stands. It is found most commonly among shrubbery at the open margins of woods, or more particularly where close-grown stands of sumach or locust, or thickets of blackberry or raspberry, prevail. Buckle (1929) has noted that female *A. antilope* frequently hunt among the leaves of locust (*Robinia pseudacacia*), and indeed I have never failed to find the wasp wherever stands of young locust occur in the vicinity of Rensselaerville.

The flower preferences of *A. antilope* are reasonably well marked. As the wasp is found from late April or early May through the summer to late September or mid-October, there is a marked succession of specially favored flowers over the season. In June and early July it visits blackberry, red raspberry, choke cherry, and especially staghorn sumach (*Rhus typhina*). Thereafter, parsnip (*Pastinaca sativa*) seems its preferred flower, to be superseded in mid-July through to mid-August by meadowsweet (*Spiraea latifolia*). Toward the season's close, the goldenrods (especially *Solidago canadensis* and *S. graminifolia*), pearly everlasting (*Anaphalis margaritacea*), and an unidentified, bushy white aster apear equally favored above all others. Robertson (1928), it may be noted, lists 14 flowers he found to be visited by *A. antilope* at Carlinville, Illinois. Only the two goldenrods, and perhaps an aster, are common to Robertson's list and the preferred flowers I have noted.

The Nesting Site

There are a number of rather slender accounts of the nesting of *A. antilope,* some of which cannot be credited to this wasp with certainty as the nesting adult was not captured for definite identification, or the brood reared to maturity. Among such I place Westwood's (1836) and the Peckham's (1905) descriptions, as well as Reinhard's (1929) account, for the last is not satisfactorily validated by the information given. Smith's (1846) description of *A. antilope* digging its nest in a sand bank is very likely based on a misidentification, and Bequaert (1944) has already discredited Strand's (1914) allegation that *A. antilope,* like *A. birenimaculatus* (Sauss.), makes free mud nests.

On the other hand there is no serious doubt as to the identity of the nests described by Malyshev (1911), Rau and Rau (1918),[2] and Rau (1928), and it was thus established that *A. antilope* makes a linearly arranged nest within hollowed stems of plants. In Rau's cases, one nest was within a woody elder twig, the other in a sumach twig that had previously been nested within by a bee, *Ceratina.* In the latter nest, it is significant that the upper portion of the burrow had apparently been enlarged by the nesting female *A. antilope.* That the wasp may use other suitably arranged cavities follows from Adlerz' (1906) record of a single-celled nest in the masonry of a vertical wall, Taylor's (1922) and Balfour-Browne's (1925) nests in glass tubes, possibly from Reinhard's (1929) observations of wasps storing caterpillars in channels between and under shingles of a well-house, from my own witnessing a similar storage of caterpillars between shingles of the porch of a large house, and perhaps also from Pierre's amusing observation of an *A. antilope* female utilizing a cavity in a window frame of a shuttle train making several trips daily between Bézenet and Doyet.[3] Furthermore, according to Bequaert (1925, p. 91),

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[2] Nevertheless the brief account by the Raus leaves much to be desired. Did they possess a mixed nest? It is hard to believe that *A. antilope* occurred within a cell but one-quarter inch long, or, as they seem to say, that a chrysid wasp and four *A. antilope* emerged from a total of four cells.

[3] Westwood (1836) claims to have observed *A. antilope* nesting within holes in rotten mortar of an old brick wall, and the Peckhams (1905) attribute a nest in the mouthpiece of a tin horn to this wasp.

Blackman and Stage have bred *A. antilope* from dead hickory wood. Finally, I have seen *A. antilope* provision and seal an old *Sceliphron* mud nest under the eaves of a cottage. In this case, *A. antilope* divided the *Sceliphron* nest into two successive cells.

The Trap Nests Inhabited by *A. antilope*

While endeavoring to discover the natural nest of *A. antilope,* time and again the female wasp was observed crawling into crevices and channels in stone foundations and walls, as well as into knot and nail holes in posts and wooden walls. At these places, and along margins of sumach and locust stands, at field margins, and in woods, 6x1x1 inch sticks of seasoned white pine having a single drilled burrow from 95-130 mm long, either 6 or 7 mm in diameter, were placed with or without cover. Wherever female *A. antilope* had been observed hunting in the immediate vicinity of a subsequently placed series of trap nests, some nests were always accepted by *A. antilope* (as well as by other wasps). Whether placed low (4 inches from the ground) or high (5 feet), with N, E, S or W exposure of the entrance, or shaded or not, trap nests were readily accepted (burrows in every case were not far from horizontal). Only nests along open fields and remote from stands of shrubs, and nests placed within close woods, were, as a class, unaccepted by *A. antilope.*

As Malyshev (1911) observed, nests of *A. antilope* constructed in tunnels consist of a linear series of provisioned cells and, as with the nests of quite a number of odynerines, the most proximal or last filled cell is separated from the entrance plug by a vestibule, or empty cell, of varying length. Mud partitions separate cells from one another, and the terminal plug is also of mud. In addition to the vestibular cell, there may be one or more unprovisioned cells placed among those that are provisioned. According to Malyshev, these exceptional cells differ from the others by having doubled end walls (*i.e.,* two successive mud partitions per end).

For the purpose of analysis, the inhabited trap nests can be placed in two series: those (series A) having a burrow 6 mm in diameter, and those (series B) having a burrow 7 mm in diameter. They are divided thus because the average volume of the burrow in the two series is very different. In A the mean volume is 2700

mm^3, in B the mean volume is 4750 mm^3, and the smallest difference in volume between any two burrows of the different series was an excess of 1850 mm^3 favoring a B nest. The dimensions of the cells of these nests are conveniently summarized in table 1. Of the 19 nests listed, 17 had been completed when taken up, and it is interesting that only one of these lacked an empty vestibular cell (*viz.*, nest 15).

It is perhaps a surprising fact that the very considerable volume differences between the burrows of the nests of the two series are not reflected in equally large compensatory differences in nest proportions. In each series there is the same average number of provisioned cells, namely 2.7, and the average total number of cells per nest is also statistically the same, namely 4 cells per nest in series A, 4.5 cells per nest in series B. The provisioned cell is long, having an average length of just over 20 mm (or four-fifths of an inch) for the 51 stocked cells of the 19 nests.[4]

As has often been noted among aculeate Hymenoptera, there tends to be a definite relationship between the size of the cell and the sex of the wasp larva that develops within it. Taylor (1922) found suggestions of such a relationship for *A. parietum* (L.) (= *tardinotus*), and Rau (1932, 1945) gives evidence of such a relationship in nests of *Rygchium foraminatum* and *A. catskill* (Sauss.). It is very likely the case for *A. antilope,* also, that female wasps on the average develop in larger cells than do males. The ten reared females (table 1) came from cells the average length of which is 22.6 mm, whereas the average length of the three cells from which males developed is but 14.3 mm. The difference, 8.3 mm, is more than 2.8 times the standard error of the difference ($\pm$ 2.93 mm), so the chance is less than 0.02 that male and female cells have equal mean lengths. This conclusion can be reached in still another, more indirect way. In multiparous eumenoid nests, the first cell almost always contains a female wasp larva, the last cell generally possessing a male larva. For the ten nests having three or more provisioned cells, the mean length of

[4] Reinhard (1929) states that each cell of the nest he examined, and which he supposed to be that of *A. antilope,* was approximately half an inch long. This suggests that some other, smaller species was under observation, perhaps *A. tigris.*

TABLE 1

Lengths in millimeters of successive cells in 19 nests of *Ancistrocerus antilope*. Note that cell-1 is the first formed or innermost, cell-2 the second formed, and so on; the total number of cells in a given nest is the sum of the cell and vestibule columns in which a length entry is made. Thus nest-1 totalled 5 cells, nest-2 totalled 3 cells, etc. Male and female signs indicate the sex of wasps reared to maturity. An asterisk (*) denotes an unprovisioned, empty cell other than a vestibular cell. Bracketted figures are *mean lengths* of burrow, *provisioned* cells and vestibule, in series A (nests 1-13) and B (nests 14-19).

	Lengths of:							
Nest #	Burrow	Cell-1	Cell-2	Cell-3	Cell-4	Cell-5	Cell-6	Vestibule
1	98	16 *	28 ♀	14 ♂	10 ♂			13
2	95	32 ♀	31					24
3	97	17 ♀	16 †					56
4	96	19	19	—	not completed		—	—
5	96	17	15	—	not completed		—	—
6	97	18	22	16	15		—	15
7	96	18	19	18	15	13		3
8	96	17	19	17	22			4
9	95	24	22	22				15
10	96	58						35
11	96	23	42 *					20
12	96	30	15	16				21
13	97	25	17	23				21
$\bar{m}_A$	(96)	(25)	(21)	(18)	(16)	(13)		(21)
14	118	25 ♀	56 *					35
15	120	21 ♀	23 ♀	24 ♀	20 ♀	19 ♂		none
16	118	28 ♀	18 ♀	24 *				33
17	135	14	18	19	14	14	20 *	15
18	120	21 *	20	17				40
19	132	12 *	17	84 *				7
$\bar{m}_B$	(124)	(22)	(19)	(20)	(17)	(16)	—	(22)

† This cell was not provisioned, nor had an egg of *A. antilope* been laid in it. A hatched chrysid egg, and mummified first instar chrysid larva, lay in the otherwise empty cell.

the first provisioned cell is 21.6 mm., that of the last 17.2 mm; the difference is 4.4 mm, or 2.2 times the standard error of the difference ($\pm$ 1.99 mm), for which $P < 0.05$. On the average, then, male *A. antilope* develop in smaller cells than do females.

The unprovisioned, non-vestibular cells upon which Malyshev (1911) has commented appear to be unusually frequent in nests of *A. antilope*. Eight cells of this sort all have single walls both anteriorly and posteriorly where they are intercalary cells (5 cases), or single walls anteriorly where they are the initial cell of the nest. On the other hand four nests (nos. 6, 7, 10, 18) have a total of 9 provisioned cells with double walls. Three of these cells are initial ones, and so have only an anterior double wall, as in only one case among the 19 nests is the inner end of the burrow walled with mud. Four intercalary cells have both anterior and posterior double walls, and one intercalary cell has a single wall posteriorly, a *quadruple* wall anteriorly. The unprovisioned cells do not differ from the ordinary provisioned cells by being set off by double walls as Malyshev found in the nest of the Palaearctic *A. antilope*. In my sample, 13% of all walls, other than vestibular anterior walls, are double, but in every case the double wall marks off provisioned cells even though such cells—like unprovisioned cells—are characteristically single walled.

In every instance the mud partitions are without any detectable vegetable matter. Use of pith in the cross-wall mortar, such as Bischoff (1927) mentions for European *A. antilope,* seems not yet to have been discovered or commented on for nests of American members of the species. Quite possibly, in the instance mentioned by Bischoff, unremoved scrapings of pith from the walls of the burrow had been fortuitously worked into the fresh mud as the wasp molded the partition. On several occasions I have observed females of *A. antilope* and *A. unifasciatus* (Sauss.) scrape up with their mandibles sunbaked, hard, dry earth from a grass-free patch (*ca.* 8 square inches in area) at the margin of a lawn and thicket. Dry earth is apparently moistened orally by the wasp, and then used directly to form nest partitions and plugs.

In general, the single partition is from 0.8 to 1.5 mm thick. The terminal mud plug that closes the entrance is, with one exception (nest 14), multilayered, and often surprisingly thick. Although terminal plugs ranged from 1.5-10 mm in thickness, on the average they are 5.5 mm thick, and made of successive, more or less juxtaposed layers which average 1 mm in individual thickness.

The position in which the egg is hung from the ceiling of the provisioned cell has been scored for the cells of 7 nests, and it ranges from a seventh (0.14) to just less than a half (0.47) of the total length of the cell, from the innermost partition. The mean length of the 21 cells scored for egg position is 20 mm, and the mean position of the egg is 5.5 mm (or 0.28 of the average cell length) from the inner wall. Binomial probability plots show that the measurements for all the 21 cells form a homogeneous collection ($P > 0.5$), and that the seven parent females that constructed these nests did not show significant differences among themselves in their egg placements.

The Prey and the Hunt

Once *A. antilope* has chosen a nesting burrow, it hangs its first egg near the end of the burrow, just as most odynerine wasps do, and then seeks its caterpillar prey. Besides the mere records that caterpillars are used (*e.g.*, Adlerz 1906; Taylor 1922; Reinhard 1929),[5] Mauvezin (1886) found *A. antilope* preying upon "chenilles de la pyrale ou tortrix du rosier",[6] and Buckle (1929) observed the wasp capturing caterpillars of the silver-spotted skipper, *Epargyreus tityrus* (but see footnote 7). Following Buckle's lead, I observed *A. antilope* capturing on locust a small, pastel-green gelechioid caterpillar that is found between leaves that it draws together. Skipper larvae were also present on these trees, but in no case did I see *A. antilope* molesting them, nor did they occur as prey among the 700-900 caterpillars of the 100 or more provisioned cells that I have so far examined. (These include observations made on an additional 41 nests to those listed in table 1.) In all I have recognized only 4 different kinds of caterpillar

[5] Ashmead's (1894) oft-quoted statement, that the Rev. T. W. Fyles observed *A. antilope* provisioning its cells with larvae of the larch saw-fly needs verification; so far as I am aware, Fyles does not seem to have published this himself. Rau and Rau (1918) are mistaken in their claim that Ashmead (*op. cit.*) holds *A. antilope* to destroy "tineina, geometrina, tortricina, pyralina and noctuina larvae in great numbers." Of course *A. antilope* may prove to do so, but Ashmead merely alludes to *Odyneri* as a group.

[6] According to Dr. Jean Pasteels, by this common name Mauvezin very likely refers to either *Cacaecia rosana* L., or *Argyrotoxa* (*Tortrix*) *hoffmannseggana* Hübn., the first being the more common species. *Vide*: Hardouin, 1943, *Le peuplement entomologique du Rosier*, Paris.

among the prey seen, and these proved to be pyralids and (probably) gelechiids, with the presumed gelechiids forming about 80% of the prey.

Mauvezin (1886) and Buckle (1929) both describe the hunt and capture of caterpillars by *A. antilope,* and my own four observations agree well with theirs, even though the actual prey and some other circumstances are different in each case. The female wasp flies rapidly about the outer branches of locust, often hovering in flight, as though inspecting the leaves before her, ultimately locating a set of two or more leaflets that the caterpillar has drawn together. The wasp alights on the stem, or leaves, and appears to work (bite?) the mid-region of the underside of the packet of leaflets, quickly and adroitly seizing and pulling out the caterpillar as it partially emerges from the apex of its abode. The wasp may immediately sting the caterpillar, or else rest with it squirming beneath its venter, apparently malaxating the region just behind the head capsule before stinging it. The inevitable stinging follows, and the wasp may deliver as few as 2, or as many as 6, separate stings (*v.i.*). According to Mauvezin and Buckle, stinging is a fairly leisurely process, but I could not be sure of the time of insertion or withdrawal of the sting, or even the number of times the sting was used, or precisely where it was inserted, for I could get no closer than 5 to 6 feet from the preying wasps. In any event, after perhaps a minute of occupation with the caterpillar, the prey is aligned beneath the wasp's venter, and the wasp drops into flight with its prey. In the four cases that I observed, the wasp removed the caterpillar from its roll of leaves on first attempt, and in no case did the caterpillar succeed in dropping to the ground. Interestingly, Mauvezin found the wasp pursues dropped caterpillars, continuing the process of their paralysis on the ground, whereas Buckle notes that the wasp abandons such caterpillars, not even following them to the ground.[7]

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[7] In view of this striking difference of observation, I have wondered whether dropped caterpillars served as Buckle's material for the identification of the prey. If so, it is possible that *A. antilope* does not provision its cells with *Epargyreus,* and certainly Buckle has not shown that it does. It may be that the wasp did not pursue the dropped skipper caterpillar precisely because it is not ordinarily its prey, having mistakenly driven *Epargyreus* from a leaf packet whilst seeking another caterpillar.

Wasps returning to their nests with prey give only fleeting opportunities to confirm others' accounts (*e.g.,* Mauvezin 1886; Buckle 1929; Reinhard 1929) that *A. antilope* carries the paralyzed prey beneath her, venter to venter, gripped with the mandibles at the thorax, and perhaps also by the mesothoracic legs during flight.[8] When the burdened wasp is walking, the caterpillar appears regularly to be held by the wasp's mandibles alone, and the impression given brings to mind an *Ammophila* with prey. Perhaps blood turgor and tergital muscular arrangement keeps the caterpillar more or less stiffly extended when in this position, for were the caterpillar's dorsum applied to the wasp's venter, the body of the prey would droop down, offering no resistance to a ventralward flexion.

Occasionally *A. antilope* females bring in caterpillars larger than they can lift into renewed flight, for when grounded before reaching the nest they are unable to become airborne again. A wasp, twice seen to ground on a large porch, with caterpillars of exceptional size projecting far beyond the abdomen, planed the burden in short hops, but failed to rise in free flight. In both cases a distance of about 16 to 18 feet was traversed, the wasp reaching the shingled wall and ascending it to her nest between the shingles.

The Sites at Which the Caterpillars Are Stung

So far as I am aware, only Mauvezin (1886) and Buckle (1929) have described the stinging of caterpillars by *A. antilope* and have attempted to observe the regions in which the caterpillar is stung. Mauvezin holds that caterpillars are stung between the true and false legs, nearly at the mid-length of the body. If the caterpillar proves insufficiently paralyzed, the wasp—after a pause—administers an additional 2 or 3 pricks in the wound, at the same time malaxating the neck of the caterpillar. Buckle maintains that the wasp stings the caterpillar ventrally in one of the front segments, the sting being deliberately applied to different places. Even though, as stated earlier, I was unable to follow the act of stinging in the few cases I witnessed, it is nevertheless possible to say quite accurately where, and how often, at least some of the

[8] Westwood (1836) observed a wasp, possibly *A. antilope,* holding with its metathoracic legs the caterpillar prey beneath its body.

caterpillars are stung. As will now be shown, the stinging takes place invariably at two points of the caterpillar's body, and only occasionally and erratically are other sites stung.

The pastel-green (presumably) gelechiid caterpillar found on locust was the caterpillar of choice for the wasps occupying my trap nests. This caterpillar is devoid of any markings of the integument when taken from its leaf nest, or from a wasp just before the act of stinging. But paralyzed prey in the nest, or taken from the wasp at the nest, have their wounds clearly marked by tiny blackened clots of blood sealing the sites of trauma. With speckled caterpillars, or ones with deep pigmentation, it may be difficult or even impossible to say for sure where they have been stung. Caterpillars from cells in which wasp larvae or mites are active also present difficulties in this regard.

When wounds of paralyzed caterpillars are closely examined, two kinds of clot are seen to occur. In one class the clot is large and disclike, as though the wound has oozed and the plasma spread. Such clots occur in rather scattered fashion on the bodies of caterpillars, and are perhaps most frequent dorsally. Several facts about these clots seem of special significance. First, some paralyzed caterpillars show none of these disclike clots; second, caterpillars having these clots show no characteristic numbers or patterns of them, or other similarity from caterpillar to caterpillar; third, such clots are most frequent on caterpillars from cells in which there are feeding wasp larvae, and least frequent among caterpillars from cells possessing unhatched eggs. These facts lead to the conclusion that such clots arise from inconstant causes, some of which at least operate long after the time at which caterpillars are stung. I believe these blackened clots mark malaxations and other traumas that have little or no direct connection with paralysis by stinging. They are characterized by their disorderly and irregular occurrence.

A second type of clot contrasts sharply with the above, appearing as a cleanly localized short streak, or small dense pinpoint of black. These clots are non-randomly distributed, occurring only ventrally in my experience, and are astonishingly constant in their position and occurrence from paralyzed caterpillar to caterpillar. Furthermore, there appears never to be less than two of these clots,

nor does the number of clots of this type increase with time as so often happens with the large, disclike sort. Without any doubt, these clots mark the sites at which the caterpillars have been stung when paralyzed by *A. antilope*.

Seventeen caterpillars from recently closed cells of *A. antilope* all possessed at least two clots of the second type, which I shall call " sting-clots ". The seventeen caterpillars had a total of 47 sting-clots among them. *All* seventeen caterpillars had at least one of their sting-clots in the metasternum between or just behind the metathoracic legs, and medially located or roughly so. In addition, *all* seventeen also had at least one sting-clot anterior to the prothoracic legs, but posterior to the hind margin of the head capsule (*i.e.*, in the ventral " neck "), and medially located or nearly so. Some caterpillars also had additional sting-clots. Two had single sting-clots between the prothoracic legs. Two other caterpillars, in addition to the metasternal and " neck " sting-clots, had erratic sting-clots elsewhere, 5 being on the pleura of the " neck ", and one on the seventh abdominal sternite.

The average number of sting-clots per caterpillar in this series is, then, 2.9. The average number of stings the wasp delivers to the caterpillar's mesosternum is 1.4, to the " neck " 1.1, and elsewhere 0.4. Twelve caterpillars were stung twice only, one was stung 3 times, one 4 times, and three were stung 6 times. There is little doubt, then, that *A. antilope* regularly and perhaps without exception stings each caterpillar (of this species, at least) at least once nearly medially in the metasternum and at least once in the " neck ". In most instances (*ca.* 70% of the time) these two stings into the vicinities of the largest ganglial masses seem sufficient to bring about a degree of paralysis acceptable to the female wasp.

The Condition of Stored Prey

The condition of the prey stored in the cells of the nest is very variable, but on the average the caterpillars are capable of violent spasms and contortions when stimulated, as Mauvezin (1886) has commented, and some caterpillars may even pupate within the cell. Until eaten, the caterpillars continue digestion of the food within their guts, passings feces to the cell floor. Occasionally one or

more caterpillars die and become foul. Such caterpillars, if adequate numbers of viable ones are present, are rejected by the feeding wasp larva, and, along with caterpillar feces, and the tough walls of the head capsule and pupal abdomen, are among the variable remains when the larval repast is done. The caterpillar ordinarily remains fresh and responsive for a surprising period of time during feeding of the host larva.

When *A. antilope's* paralyzed caterpillars are not fed upon, they recover to a considerable extent their capacity for directed movement. In the case of one nest of *A. antilope,* the female wasp failed to return after sealing the initial cell in the usual way. The egg of this cell failed to hatch, and 5 days after the cell had been closed the caterpillars burst the mud partition, floundered to the entrance, and some dropped to the ground below. The egg still hung intact from the roof of the cell when examined, having physically survived the struggles of the prey enclosed with it. Whether the egg had a lethal genetic constitution, or was internally damaged by the caterpillars, cannot be known, but it is difficult to agree with the Peckhams (1905) that the anchoring filament is especially beneficial in protecting the egg from struggles of the prey. Certainly an egg not free to move beyond a small limit should be a bad risk if struggling prey can damage it by movements alone.

Eggs detached and placed among the prey may hatch in the usual way, and with no evident damage, as Taylor (1922) before me has also noted. Perhaps suspension is important in preventing the egg from being worked into the vicinity of a caterpillar's jaws, and its position in the cell is compatible with this view, but other interpretations come to mind. For example, assured vertical suspension may guarantee that morphogenetic substances in the egg will not be displaced during stages of earliest embryogenesis, which take place while the cell is being stored. In any event, the issue can only be settled by experiment. Curiously enough, Bristowe (1948) found the egg of *Odynerus spinipes* (L.) to be hung by a thread from the ceiling of the nest, yet in two cases of the very closely related *Odynerus laevipes* Shuck., Bristowe found the egg at the bottom of the cell, among the larval prey, unprovided with a thread and not suspended in the usual way. If Bristowe's observations on *O. laevipes* are generally confirmed,

egg suspension in this species (at least) would seem to have lost its selective value.

Provisioning of the Nest

Malyshev's (1911, fig. 15) photograph of an opened nest of *A. antilope* gives an excellent impression of the manner in which this wasp stuffs its cells with caterpillars. In some nests with long cells, the paralyzed caterpillars lie in orderly, nearly parallel arrangement, heads to either end. In shorter cells the caterpillars are packed in more disorderly fashion, some encircling the wall of the cell, others folded on themselves, and so on. The number of caterpillars per cell varies widely with the species and instars used, as well as more slightly with the absolute size of the cell, cells of female larvae usually being provided with a slightly greater bulk of prey. In some cases more than one species of caterpillar may be used, pyralids and even (presumed) gelechiids, for example, have been found together in single cells of *A. antilope*. Such simultaneous use of different species becomes more common among late August's and September's wasps, and probably reflects a waning of the populations of potential prey available. At any period, however, it is common to find several different instars represented among the caterpillars of a single cell. The smallest number of caterpillars that I have found in a closed cell is 4 (*cf.* Adlerz, 1906; Taylor, 1922), the largest number is 15, and the mean number for all cells is nearly 9.

The length of time required to provision and complete a nest varies with the weather and season, as well as the number of cells stored. Taylor (1922) observed *A. antilope* slacking off its nest preparations during very hot spells, and I have noted the wasp taking more than a week to provision a three-cell nest during an early September cold spell. When work is in abeyance, whether because of low or high temperature, or nightfall, the wasp remains resting within the bore of the nest, head facing outwards.

Four nests for which I have exact records contained a total of 12 provisioned cells, and took just under an aggregate of 12 days to complete. The most rapid construction and provisioning that came to my notice was a nest (no. 76) containing 5 provisioned cells, that was built in the first two days of July. Very likely, all

things considered, one cell per day is close to the true average rate of nest construction and provisioning. From the little that is known of the longevity of *A. antilope* females (*v.* Taylor, 1922), it may be guessed that the average female provisions about two dozen cells in her lifetime, and probably less than twice that number represents the maximum effort of a female under the most favorable conditions that are likely to prevail.

A Timetable of *A. antilope's* Developmental Stages

The egg of *A. antilope* is about 2.8 mm long, 0.9 mm wide, slightly bowed in side view, and hangs from a stalk that averages about 0.7 mm in length. The larva grows ultimately to a length of 14 to 18 mm, and is from 4 to nearly 6 mm in greatest girth at the time of cocooning. It is thus very much larger than the larvae of any of our other *Ancistrocerus,* or that of *Rygchium foraminatum.* During larval growth there are not less than three moults, nor more than five, but the exact number has not been worked out. After feeding is completed, the larva spins a cocoon, as Taylor (1922) has already noted. Whether the cocoon (which may be quite thin) is ever absent, as Rau (1928) believes, I do not know, but more than 70 *A. antilope* larvae that had passed their meconia have been examined by me, and in every case the larva was enclosed within a cocoon. The cocoon may be whitish, greyish, yellow, or of a rich golden brown tinge. Ordinarily the meconium is passed only after cocooning is complete, but in one case a larva cast its meconium during its spinning. In only one case, among the more than 70, was the meconium cast to the anterior, rather than to the posterior, end of the cell, with the pupa's head directed away from the path of eventual exit.

Within a day or two after the meconium is shed, the thoracic region of the prepupa becomes noticeably set apart from the head and abdomen by slight, yet well-marked, constrictions. A day or so thereafter, but before the larval integument is shed, the posterior margin of the compound eye of the forming pupa may be seen through the larval integument as a pink or violet crescentic streak on each side. The eye crescents are located in the apparent (but false) first post-cephalic segment, that is, between the posterior lateral rim of the head capsule and the first (prothoracic) segment bearing spiracles.

When the larval exuvium has been cast, the body of the pupa is translucent white, and dorsally bears many small spinous elevations —especially on the abdomen. The protruding 10th abdominal tergite of the fully formed pupa is bluntly rounded apically, and its form allows an easy separation of the pupa of *A. antilope* from that of *A. tigris* or *R. foraminatum*. This pupal tergite forms an elongated spine in ventral view in both of the latter species.

The pupa develops a deep blackish-brown pigmentation of the compound eyes, and an amber-cinereous tingeing of the forewings, before the coloration of the body sets in. The black coloration of the integument first appears suffusely on the mesonotum, dorsally spreading anteriorly and posteriorly over the thorax, vertex, and abdomen, and down over the pleura. Ventrally the blackening spreads in the same manner, but everywhere follows in time the pigmentation of the corresponding dorsal regions. Future yellow bands and markings first appear translucent whitish grey until blackening of the integument is virtually complete. Then these areas turn pale greenish yellow, then a naples yellow, and finally the bright pure yellow of the freshly emerged adult.

The pupal integument becomes loose, wrinkled, and moist within, once the yellow coloration is complete. A day or so later, the adult casts the pupal integument in a matter of hours. The teneral adult remains in its cocoon for two or three days, and it ordinarily takes this time for the wings to lose their callow appearance. If stimulated, such a resting, teneral adult will exude a large drop of clear fluid from its mouth. There is little doubt that this fluid normally serves to soften the hard, dried mud end walls of the cells as the young adult cuts its way to the outside. Although I have not witnessed events, at the actual moment of cutting open the mud plugs, at exodus from the nest by *A. antilope,* I have seen them at the emergence of another vespid, *Pseudomasaris vespoides* (Cress.). In the latter case, as the exit hole is cut, the excessively hard, sun dried mortar of the nest is softened by the emerging wasp which pumps from its mouth a clear fluid onto the mortar.

The moisture between the pupal envelope and the eclosing wasp's integument is necessary for successful emergence. A wasp may shed the pupal exuvium and expand its wings even when the pupa lays on a glass surface or hard cloth, but fails to complete

normal eclosion if placed on an absorbent surface such as Kleenex. It seems likely that the varnish applied to the cell by the cocooning larva provides not only a base upon which threads of the cocoon will stick, and a waterproofed finish against entrant moisture, but that it also helps prevent uptake of moisture by the cell walls at the critical period during which the pupal exuvium is cast.

Ordinarily, if diapause has not occurred, the adult wasp ecloses 29 to 35 days after deposition of the egg. Inhabitants of nests made by wasps during mid-July, and thereafter, normally (but not invariably) enter diapause, whereas those of nests constructed earlier almost never do. So far as duration of stages is concerned, there was no detectable difference in duration of developmental stages, through to shedding of the larval meconium, between individuals that diapaused, and those that did not. Table 2 provides a general timetable for the developmental stages of *A. antilope* at an overall average temperature of approximately 20°C (68°F). Diapause sets in after the meconium is shed, and sometimes after the thoracic region of the prepupa is delineated, but, in all the cases I have observed, before the eye crescent is visible. It remains to be seen whether the tabulated times for stages following the shedding of the meconium may be applied to individuals in which diapause has broken. Finally, it may be noted, Taylor's (1922) few observations correspond very well with the figures given in table 2.

A final point of interest is that female *A. antilope,* reared from cells of trap nests and which have had no food as imagos, will mate with males within 3.5 days of casting the pupal exuvium, and perhaps even sooner. This means in effect that the female wasp is ready to mate at the moment of emergence from the nest. Details of the mating process, and its extraordinary role in the association between the wasp and the mite, will be dealt with in the second paper of this series.

The Number of Generations Per Year

Mauvezin (1886) found two generations per year of *A. antilope* in Europe, and Taylor (1922) argues that our own *A. antilope,* along with *A. parietum* and *A. catskill albophaleratus,* also has two generations per year. If Balfour-Browne (1925) had an adequate

TABLE 2

Timetable of developmental stages of *Ancistrocerus antilope*. In the first column is given the mean day, from the time of egg laying, at which each stage is reached. The second column gives the range in days each successive stage requires; *e.g.*, the egg stage takes from 2 to 4 days, cocooning takes from 2 to 4 days, the meconium is usually shed from 1 to 2 days after the cocoon has been completed, and so on. The third column gives the number of cases upon which the observations were made.

Developmental Stage	1 Average Day of Occurrence	2 Range in Days Elapsing	3 Number of Cases
Hatching	2.5	2–4	4
End of feeding	8.5	5–7	7
Start of spinning	9.5	1	13
Cocoon finished	12.5	2–4	9
Meconium shed	14	1–2 *	9
Pupa free, larval exuvium cast	18	3.5–4.5	7
Black coloration complete	28	9–13	5
Yellow coloration complete	31	2–4	5
Pupal exuvium shed	33 †	1–2.5	9

* In one case the meconium was shed in the mid-period of active spinning.

† Nine wasps had the following days of eclosion: 29 (♂), 30 (♀), 31 (♀), 31 (♀), 32 (♂), 32 (♀), 32 (♀), 33 (♀), 35 (♀).

sample of nests, it seems that *A. antilope* has but one generation per year (at least some years) in England.

At Rensselaerville there were assuredly two generations per year in 1951 and 1952, and possibly three. Seven of nine nests closed by the wasp before July 21 gave forth their broods in early to mid-August, a time at which there is normally a new peak of freshly emerged males and females in the natural population. Two nests closed in the first and second weeks of July, however, did enter diapause, just as the Raus' (1918) nest collected on a July 12. All of some 30 nests closed after the onset of August entered diapause. The wasps coming from these nests constitute a second generation, which in turn provisions nests chiefly in August and September. These second generation nests, for the most part, overwinter to give the first generation of the following year. But perhaps some of the progeny of the second generation do emerge in September, without an intervening diapause. Although none

of my trap nests have behaved in this way, both in 1951 and 1952 I have taken freshly emerged male and female *A. antilope* during the first and second weeks of September. As *A. antilope* is provisioning nests at that time, it is possible that a rather small third generation contributes to the overwintering population.

Mortality in the Nest

Six of the nests of table 1 had been parasitized or ravaged by another insect. *Melittobia chalybii* Ashm. was present in nests 2 (cell 1) and 7 (cell 5). Interestingly enough, in both cases single adult females were present in the cells, and their broods had not yet destroyed the hosts. *Chrysis* (*Tetrachrysis*) *nitidula* Fab. was reared from nests 7 (cells 2 and 4) and 17 (cells 3 and 4), and a hatched chrysid egg and its mummified larva lay on the floor of cell 2 in nest 3. Perhaps, in this last case, *A. antilope* discovered the egg of the parasitic wasp before laying its own, for the egg of the chrysid had been enclosed as sole occupant of this cell. Is this a clue to the origin and significance of the empty, non-vestibular cells that interested Malyshev? The asterisked empty cells in table 1 contained no eggs or other stages of chrysids or other arthropod parasites, to my knowledge, but may well have possessed spots of mold spores, or other potentially mortal agents, that the nesting wasp thus isolated by enclosure.

Nests 4 and 5 attracted attention in the field by the dropping of caterpillars from their entrances, and finally (nest 4) of an *A. antilope* larva. When taken up, each of these nests had an open meshwork dome closing its entrance. Ironically, in each case a large, spotted caterpillar (probably gelechiid!) had entered the nests before the mother wasps had closed the entrances, and cleaned out both provisional cells of nest 4, and the second cell of nest 5. In the latter nest the cocooned larva almost certainly would not have succeeded in emerging, for the caterpillar had densely webbed over the anterior mud plug of the unravaged cell with a network of coarse, very tough silk. In both cases the caterpillar prepared its pupal chamber in the burrow of the nest, after closing the nest's entrance with a characteristic, complexly woven series of net-like fabrics, the inner portions of which call to mind the skeletal structure of a bath sponge.

Wasps developing in ten of the 50 provisioned cells of the 19 nests were accordingly doomed by other insects. In addition to these losses, all three cells of nest 9 had the prey foul, with subsequent death of the wasp larvae. Unaccountably, or perhaps owing to genetic lethals, the wasp larvae blackened and died during feeding in cell 2 of nest 2, and cells 1, 2 and 3 of nest 8, even though the prey remained fresh. In nest 19, the single larva quickly underwent liquefaction just after it had completed its cocoon. All told, at least 18 (or 36%) of the 50 eggs of the 19 nests would not have contributed to the next generation of nesting wasps. If these nests had not been collected, it is very likely that other mortality factors would have reduced survival still further.

If, on the average, a single female has provisioned 24 cells in her lifetime (see p. 28), and if the sexes are roughly equal in numbers, it may be guessed that not more than 5 or 6 daughters represent her contribution to the population of the next generation of wasps. With a stable wasp population, then, mortality rates are high, and probably the total premature mortality is nearly equally divided between immature and adult wasps.

Competition

Ancistrocerus antilope, A. tigris and *Rygchium foraminatum* are the three most abundant eumenine wasps in the area studied, together constituting 51% of the census sample (see p. 15). Very interestingly, they frequent the same flowers, hunt the same caterpillars on locust trees (and presumably other plants), and all nest in 6 mm burrows placed along locust groves, sumach stands, or briar thickets. Furthermore all are nesting at the same periods, have at least two generations per season, and take an average of 32 or 33 days from egg to adult. These wasps, then, are in mutual competition for the most important elements of their existence.

A. tigris also nests in burrows down to 4 mm in diameter, whereas *A. antilope* and *R. foraminatum* are physically excluded from use of such narrow nesting sites. Both *A. antilope* and *R. foraminatum* will use burrows 7 mm in diameter, and perhaps larger, but *A. tigris* did not nest in 7 mm burrows. Whether *A. antilope* and *R. foraminatum* show certain specific biases in their choice of nesting sites, my experience has been too meager to tell.

But the observations carried out certainly suggest that there are no complete differences in the ecologies of the three wasps, and that some percentage of the populations of each species are in fact in absolute competition with one another in a given community. The degree to which each species has a statistical bias, or somewhat different spectra of prey and nesting sites, for example, will give some measure of the relaxation of competition between them. The trap nest technique offers an attractive approach to the working out of this problem.

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